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Poor environmental tracking can make extinction risk insensitive to the colour of environmental noise

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The relative importance of environmental colour for extinction risk compared with other aspects of environmental noise (mean and interannual variability) is poorly understood. Such knowledge is currently relevant, as climate change can cause the mean, variability and temporal autocorrelation of environmental variables to change. Here, we predict that the extinction risk of a shorebird population increases with the colour of a key environmental variable: winter temperature. However, the effect is weak compared with the impact of changes in the mean and interannual variability of temperature. Extinction risk was largely insensitive to noise colour, because demographic rates are poor in tracking the colour of the environment. We show that three mechanisms—which probably act in many species—can cause poor environmental tracking: (i) demographic rates that depend nonlinearly on environmental variables filter the noise colour, (ii) demographic rates typically depend on several environmental signals that do not change colour synchronously, and (iii) demographic stochasticity whitens the colour of demographic rates at low population size. We argue that the common practice of assuming perfect environmental tracking may result in overemphasizing the importance of noise colour for extinction risk. Consequently, ignoring environmental autocorrelation in population viability analysis could be less problematic than generally thought.

Keywords: climatic variability; demographic and environmental stochasticity; noise filtering; nonlinearity; population viability analysis; temporal autocorrelation

1. INTRODUCTION

Autocorrelated time-series are generally described by their spectral colour, with red variations being positively autocorrelated resulting in low-frequency fluctuations and blue variations being negatively autocorrelated reflecting high-frequency fluctuations, whereas white noise is uncorrelated [1]. Many abiotic environmental variables, such as temperature, are temporally autocorrelated (often showing a reddened spectrum [2,3]). Biotic environmental variables, such as resource or prey abundance, are also likely to have coloured noise properties, as many time-series of population size exhibit temporal autocorrelation [4,5]. Demographic rates depend on the environmental conditions and consequently coloured environmental noise can cause demographic rates also to be temporally autocorrelated, which in turn can affect population dynamics.

The idea that temporal autocorrelation in the environment can affect important aspects of population dynamics is widely accepted [1,6–11]. In a simple population model with neither density dependence nor age or stage structure, increasing environmental autocorrelation is expected to increase the variance of long-term population growth, leading to an elevated extinction risk in red environments and a reduced risk in blue environments [7,12]. Results from simulation studies have corroborated existing theory (e.g. [13]), but have also shown that when more complexity is included, results can be quite different (e.g. [11]). Density dependence and population structure can also produce autocorrelation in the population dynamics, and when they interact with each other and with environmental noise their population dynamical consequences are difficult to predict [14]. Overall, simulation studies show that effects of environmental noise colour on extinction risk may depend on the type of life history [15,16], density regulation [17–19], spatial structuring [17,20] and the level and type of noise-generating process [18,19,21,22].

The existing literature—albeit biased towards simple life histories and models—provides a qualitative understanding of how coloured environmental noise can affect extinction risk. However, evidence from theoretical studies that noise colour can affect extinction risk does

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not necessarily imply that noise colour will be a major determinant of extinction risk in the wild. When performing population viability analysis to assess the extinction risk of specific populations or species, we are generally more interested in the relative importance of a specific factor compared with other factors [12,23]. Below we discuss three issues that have so far been largely ignored, but we think are critical for assessing the relative importance of noise colour on extinction risk.

First, little is known about how the colour of environmental noise is tracked by demographic rates. The basic idea is that environmental noise acts via the demographic rates to affect population numbers. Nevertheless, virtually no studies specifically incorporate autocorrelation in the environmental variables (but see [24]); instead they include autocorrelation directly into the demographic rates. By doing so, it is implicitly assumed that demographic rates perfectly track the colour of the environment, which may be reasonable when one is interested in the qualitative effects of noise colour on population dynamics, but less useful for assessing its quantitative effects. Moreover, by explicitly modelling how demographic rates depend on specific environmental variables [25] and by accounting for other sources that cause demographic rates to vary over time (e.g. residual environmental noise and demographic noise), we might gain novel insights into factors that determine how well demographic rates track the environmental colour. A likely reason why this has not been done before is that long-term datasets—spanning decades for birds and mammals—are needed to decompose the temporal variance of demographic rates reliably [12,26].

Second, many studies have suggested that noise colour affects extinction risk primarily at high (positive or negative) values of temporal autocorrelation in demographic rates (e.g. [15–17]). Thus, besides explicitly modelling how the colour of environmental noise determines the autocorrelation in demographic rates, it is also important to know what values of environmental autocorrelation are realistic in the wild. As Vasseur & Yodzis [3] advocated, the first step in quantifying the impact of noise colour should therefore be to evaluate the natural range of autocorrelation in the key environmental variables that affect the demographic rates.

Third, to our knowledge, no studies have compared the relative impact on extinction risk of changes in the colour of environmental noise in comparison with other aspects of environmental fluctuations, such as changes in the mean or interannual variability. Such knowledge is currently relevant, because climate change and human actions are causing the mean [27] and variability [27,28] as well as the colour [29–31] of environmental variables to change. It has even been suggested that an increasing temporal autocorrelation and variability might be an intrinsic property of climate systems approaching a critical tipping point [32,33]. Changes in each climate aspect (mean, variability or noise colour) may affect population dynamics via different mechanisms and can result in either higher or lower extinction risk [12,34,35]. Consequently, for predicting the impact of future climate change, we need to identify which aspect of change in environmental variables is most important, and under which circumstances. Interestingly, two studies suggested that for certain parameter conditions and model assumptions, the growth rate of populations might be more sensitive to noise colour than to interannual variability [36,37] and it was proposed that this may also hold for extinction risk [37].

Here, we will investigate the relative impact of changes in noise colour of a key climatic variable, winter temperature, on the demographic rates and extinction risk of Eurasian oystercatchers (*Haematopus ostralegus*), a strongly declining shorebird species [35]. Previously, we used 24 years of demographic data to identify how oystercatchers' survival and fecundity depend on winter temperature and other environmental variables [35]. We showed how this population's extinction risk depends on both the mean and interannual variability of winter temperature, but ignored the role of environmental autocorrelation (noise was assumed to be white). However, regional winter temperatures are known to be temporally autocorrelated [29], which is expected to affect oystercatchers' extinction risk.

The availability of long-term climatic as well as demographic data and a stochastic population model now provide the unique opportunity to investigate (i) how demographic rates track the colour of the environment and how this is affected by nonlinear demographic responses, multiple sources of environmental stochasticity and demographic stochasticity, (ii) whether noise colour affects oystercatchers' extinction risk for autocorrelation values that are historically realistic (i.e. across the range of winter temperature autocorrelations observed over the past 275 years), and (iii) whether noise colour is an important determinant of extinction risk compared with the mean and interannual variability of temperature. We will show that noise colour affects oystercatchers' extinction risk, but that the absolute effect is weak in our model, especially compared with the impact of changes in the mean and interannual variability of winter temperature. We identify three mechanisms that can cause demographic rates to track the colour of environmental noise only poorly, and we argue that these are likely to buffer the impact of noise colour on extinction risk in many species.

2. METHODS

(a) *Study species and population*

Oystercatchers are long-lived (up to 40 years) monogamous shorebirds and their demography exhibits distinct age, stage and spatial structure [38]. Annual survival increases progressively from fledging to sexual maturity at the age of 3 years. Many adults are non-breeders owing to habitat saturation [39]. Breeders in high-quality habitat produce two to three times more offspring annually than pairs in low-quality habitat owing to differences in feeding ecology [40]. Consequently, six life stages can be used to describe the main sources of within-year variation in demographic rates (figure 1*c*).

From 1983 to 2007, we studied a breeding population of oystercatchers on the Dutch island of Schiermonnikoog (53°29′ N, 6°14′ W), which is declining by approximately 5 per cent per year [35]. An intensive colour-ringing programme was initiated to mark all non-breeders, breeders and offspring. Each breeding season (May–August) population numbers were counted, and we recorded which individuals were alive and what their stage-class and reproductive output were (approx. 300 marked individuals; approx. 100 breeding territories annually [39,40]).

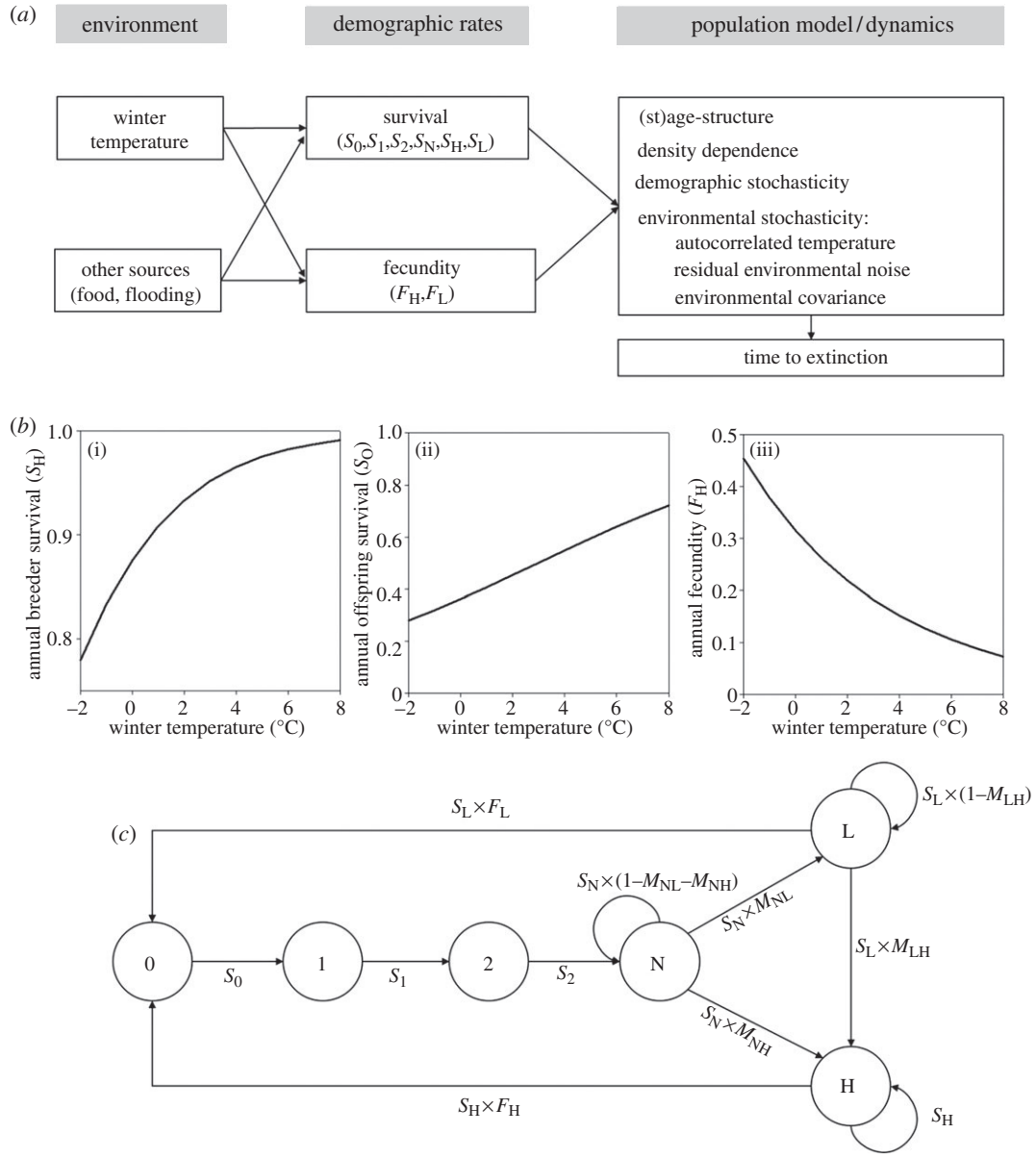

Figure 1. (*a*) Overview of how the environment affects oystercatchers' demographic rates and the population model used to estimate how the colour, interannual variability and mean of winter temperature will affect extinction risk. (*b*) The (i) concave, (ii) linear and (iii) convex relationships between winter temperature and annual breeder survival, offspring survival and fecundity. (*c*) The age-, stage- and spatially structured life cycle used in the demographic model and the stage-dependent demographic rates fecundity (F), survival (S) and movement probabilities between states (M; e.g. M_{LH} is the annual probability of movement from state L to H, conditional on survival). Six states are distinguished: 0, fledged offspring; 1, 1 year-old juveniles; 2, 2 year-old juveniles; N, adult non-breeders; L, breeders in low-quality habitat; H, breeders in high-quality habitat.

(b) *Environmental dependency of demographic rates*

Winter severity is thought to be a key environmental driver in oystercatcher populations [41–44]. We have previously shown that winter temperature can explain 32–46% of the between-year variation in each of the demographic rates in our study population [35]. Survival in all stage-classes is positively associated with temperature, with offspring survival showing a linear relationship (S_0; figure 1*b*(ii)), and survival in all other stage-classes showing nonlinear relationships (concave; figure 1*b*(i)). In contrast, fecundity in both high- and low-quality habitat is negatively associated with winter temperature, again showing a nonlinear relationship (convex; figure 1*b*(iii)). Other environmental sources (food stocks and flooding events) were also found to affect the between-year variation in demographic rates, and substantial unexplained variation remained (29–68% [35]). Recruitment M_{NL} and M_{NH} and breeder dispersal M_{LH} (figure 1*c*) are density dependent, since they are constrained by the number of vacant territories in this despotically territorial species [35].

(c) *Historical temperatures*

From 1735 to 2010, temperatures were recorded at weather station 'de Bilt' [45]. Annual mean winter temperature (December–March) at de Bilt is tightly correlated with winter temperature on the study island 165 km northwards ($r = 0.95$; 1972–2010), but slightly colder (temperatures of de Bilt were adjusted accordingly before use in the population model).

The 275-year temperature time-series was analysed using autoregressive moving average models [46] and spectral analysis in R 2.10.1 [47]. A previous climatological study

by Hurrell & van Loon [29] showed that the winter North Atlantic Oscillation index and winter temperature in north-west Europe exhibit strong covariance and spectral coherence and have both changed colour from white to red during the twentieth century. In accordance with Hurrell & van Loon [29], winter temperatures at de Bilt were also likely to be different from white noise (Ljung–Box test; $p < 0.01$). Following the approach of Hurrell & van Loon [29], we subsequently used a sliding time-window approach to investigate temporal changes in fluctuations at various values of periodicity (2–15 years). We found no strong evidence that winter temperature in The Netherlands exhibits long-term periodic fluctuations and therefore we henceforth focus on 1 year lag autocorrelations. To assess the probability that a directional change over a 275 year period in the colour of temperature could occur by chance, we compared the observed directional change in autocorrelation-coefficient with those of 10 000 generated random time-series using a first-order autoregressive function in which the underlying 1 year lag autocorrelation was constant over time.

(d) *Modelling temperature time-series*

Annual mean winter temperature (w) in The Netherlands follows a left-skewed distribution, which van de Pol *et al.* [35] showed can be approximated by:

$$w \sim c - \text{lognormal}(\mu, \sigma), \tag{2.1}$$

with

$$\mu = \ln(c - E(w)) - \frac{1}{2}\ln\left(1 + \frac{\sigma_w^2}{(c - E(w))^2}\right) \tag{2.2}$$

and

$$\sigma = \sqrt{\ln\left(1 + \frac{\sigma_w^2}{(c - E(w))^2}\right)}. \tag{2.3}$$

This parametrization specifically allowed us to vary the expectation ($E(w)$) and the interannual variability of winter temperature (σ_w) independently. During the oystercatcher study period, the mean temperature was $E(w) = 3.7$ and the interannual standard deviation was $\sigma_w = 1.7$, with rescaling constant $c = 10$.

Using standard methods [11,16,17,19], we extended the above temperature model to enable the generation of autoregressive noise of varying degrees of 1 year lag autocorrelation. Following equation (2.1), we assumed that winter temperature in year t is given by:

$$w_t = c - \exp(\mu + \sigma \times \varphi_t), \tag{2.4}$$

where φ_t follows a first-order autoregressive process:

$$\varphi_t = \alpha_w \times \varphi_{t-1} + \gamma \times \varepsilon_t. \tag{2.5}$$

In this recurrence relation, α_w is the 1 year lag autocorrelation of winter temperature and ε_t is a standard normal random variable with no temporal autocorrelation. Stabilizing the stationary variance by $\gamma = \sqrt{1 - \alpha_w^2}$ ensures that the variance of temperature is kept constant when the autocorrelation is varied, which allows us to investigate the effects of autocorrelation *per se* [16]. Wichmann *et al.* [22] have argued that the extinction risk can depend on the specific method used for stabilizing the variance of the autoregressive process. However, using spectral mimicry [48] to stabilize the variance resulted in virtually identical outcomes. Note that even when the variance of the temperature process is kept constant, changes in autocorrelation can still affect the variance of the long-term population growth, and thereby extinction risk.

(e) *Oystercatcher population model*

The technical details of the oystercatcher population model are described in van de Pol *et al.* [35]; here, we summarize its main characteristics (figure 1). The asexual stage-structured stochastic population model has the form [49]:

$$\boldsymbol{n}_{t+1} = \boldsymbol{A}_t \times \boldsymbol{n}_t, \tag{2.6}$$

where $\boldsymbol{n}_t$ is the vector of stage sizes at time t. The elements of the projection matrix $\boldsymbol{A}_t$ are realizations of the stochastic variables that represent the demographic rates. Equation (2.6) can be expanded to a post-breeding census model that includes the age-, stage- and spatial-structuring of the life cycle described in figure 1*c*:

$$\begin{pmatrix} n_0 \\ n_1 \\ n_2 \\ n_N \\ n_L \\ n_H \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 0 & 0 & S_L F_L & S_H F_H \\ S_0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_2 & S_N(1 - M_{NL} - M_{NH}) & 0 & 0 \\ 0 & 0 & 0 & S_N M_{NL} & S_L(1 - M_{LH}) & 0 \\ 0 & 0 & 0 & S_N M_{NH} & S_L M_{LH} & S_H \end{pmatrix}_t \times \begin{pmatrix} n_0 \\ n_1 \\ n_2 \\ n_N \\ n_L \\ n_H \end{pmatrix}_t. \tag{2.7}$$

The demographic rates fecundity (F), survival probability (S) and movement probability between stages (M) that determine the matrix elements change from year to year owing to density dependence and both environmental and demographic stochasticity. We included a ceiling for the number of high- and low-quality territories to account for the fact that breeding habitat is a limiting resource ($\max(n_H) = 60$, $\max(n_L) = 150$), which ensures that recruitment M_{NL} and M_{NH} and breeder dispersal M_{LH} are density dependent in a similar fashion to that observed in the field (see the electronic supplementary material, appendix S1 for details and rationale). Besides the variable of interest, winter temperature, mean demographic rates also varied as a function of other environmental factors (food stocks and flooding events [35]). Moreover, additional unexplained residual environmental variance within and covariance between mean demographic rates existed, which was modelled as multi-variate random white noise. The expressions determining the between-year expectation, variance and covariances of the stochastic variables F, S and M and their

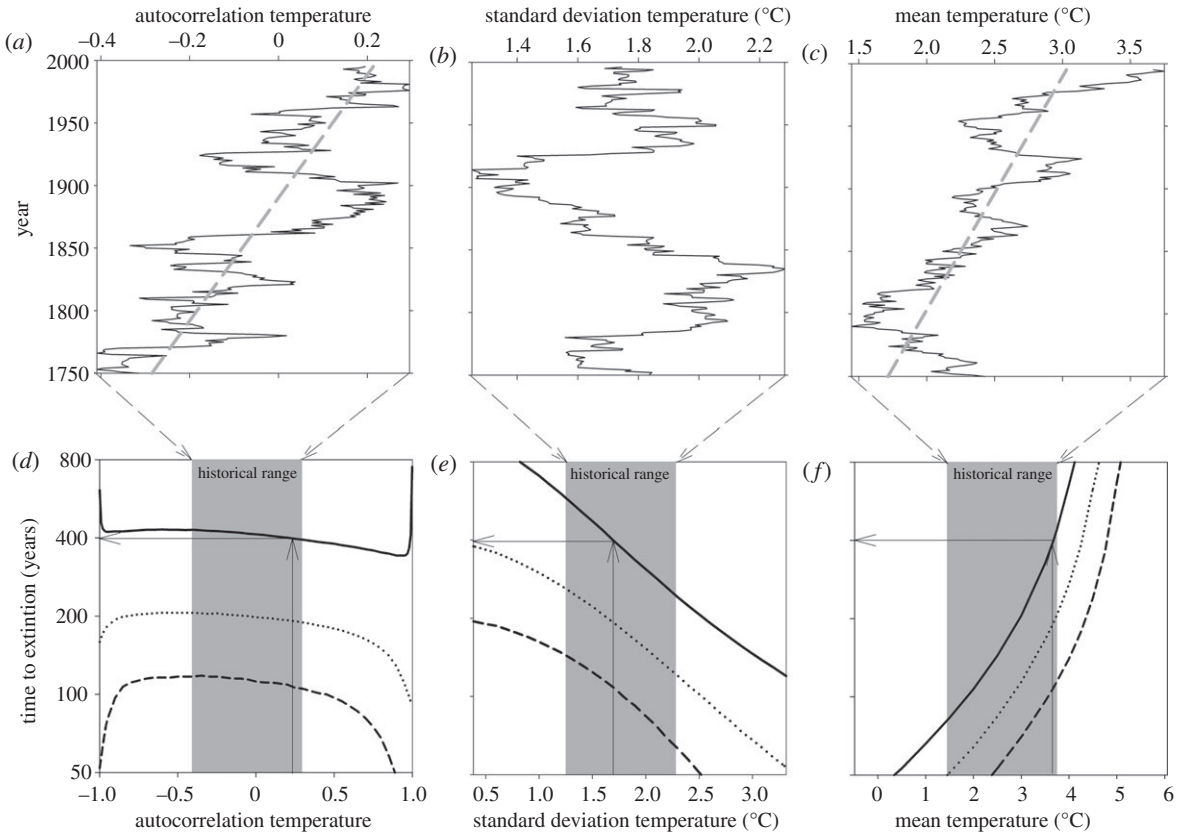

Figure 2. Historical range of (*a*) 1 year lag autocorrelation, (*b*) interannual standard deviation and (*c*) mean of winter temperatures from 1735 to 2010 in The Netherlands as described by 30 year sliding windows. The grey dashed lines depict linear temporal trends. Time to extinction for oystercatchers as a function of the (*d*) autocorrelation, (*e*) standard deviation and (*f*) mean of winter temperature, where solid, dotted and dashed lines depict the times at which, respectively, 50% (median time to extinction), 10% and 1% of all simulated populations were extinct ($n = 0$). The solid arrows in the bottom panels reflect the average temperature conditions in the oystercatcher study period (1983–2007) and point to the corresponding median time to extinction. The grey areas describe the historical ranges observed in the top panels.

dependency on density, winter temperature, food, floodings and residual environmental noise are given in the electronic supplementary material, appendix S1. Demographic stochasticity was included by assuming that realized individual reproduction and survival in a given year followed a Poisson and binomial distributions, respectively.

(f) *Extinction risk*

Time to extinction for various values of autocorrelation (α_w), interannual variability (σ_w) and mean winter temperature ($E(w)$) was evaluated by computer simulation of the population model. The observed numbers in the stage-classes in the last year of study were used as initial values. In each simulation, the initial winter temperatures were randomly drawn from the stationary temperature distribution. We determined the number of 'years' it took for given proportions of 300 000 simulated populations to go extinct ($n_t = 0$). For example, if the time of extinction for the 10% percentile was estimated to be 100 years, this means that after 100 simulated years, 30 000 out of 300 000 populations were extinct, and thus the probability of extinction within the first 100 years is 0.1. Previously, we showed that years with warm winters result in high survival and low fecundity (figure 1*b*), but most importantly that the median (50% percentile) time to extinction increases with mean temperature [35]. Consequently, in the context of oystercatchers, good conditions refer to warm winters, while bad years refer to extremely cold winters.

3. RESULTS

(a) *Historical temperature patterns*

The colour, interannual standard deviation and mean of winter temperature fluctuated substantially over the past 275 years (figure 2*a–c*; see the electronic supplementary material, appendix S2 for similar results using sliding windows of different length). The colour of temperature also changed directionally over time from blue via white to red (figure 2*a*). This directional trend from 1735 to 2010 in autocorrelation-coefficients of temperature was unlikely to be generated by chance, because simulated coloured time-series with an underlying autocorrelation that was constant over time rarely produced a similar directional trend over such a long period ($p < 0.001$). The interannual variability did not change systematically over time (figure 2*b*). However, mean winter temperatures have increased over the past centuries (figure 2*c*). De-trending the temperature time-series barely affected the autocorrelation patterns (not shown), suggesting that rising temperatures contributed little to changes in colour.

(b) *Does noise colour increase or decrease time to extinction?*

Time to extinction decreased as the colour of temperature was changed from white to red (figure 2*d*). Furthermore, as the colour of temperature was changed progressively from white to blue, time to extinction first increased but

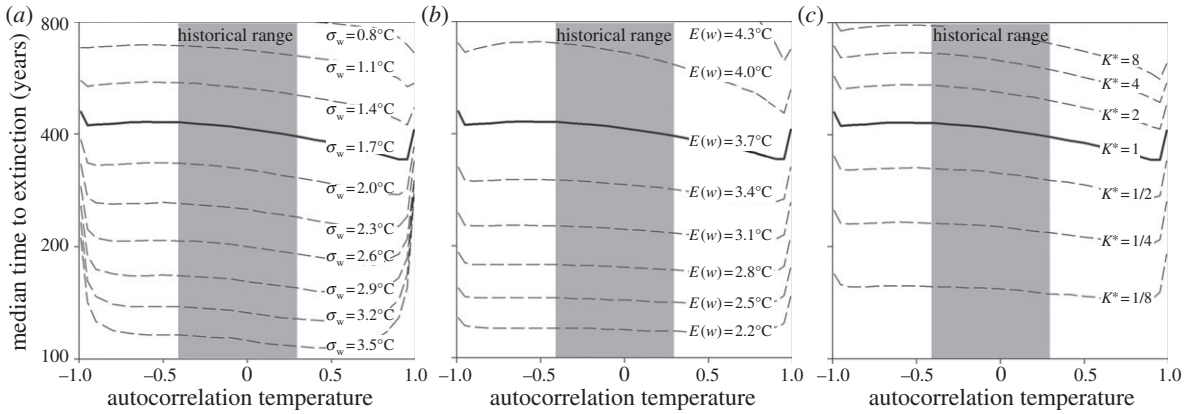

Figure 3. The effect of noise colour on median time to extinction over a wide range of parameter values of (*a*) the interannual variability of winter temperature (σ_w), (*b*) the mean winter temperature ($E(w)$) and (*c*) a measure of carrying capacity (K^*). Solid lines refer to the parameter conditions in the oystercatcher study period; the grey areas depict the historic range of autocorrelation values (figure 2). $K^* = 1$ corresponds to $\max(n_H) = 60$, $\max(n_L) = 150$ and an initial population size of 116 females; $K^* = 2$ corresponds to $\max(n_H) = 120$, $\max(n_L) = 300$ and an initial population size of 232, etc. Note that for $E(w) \geq 4.3$°C simulated populations rarely go extinct (figure 2*f*).

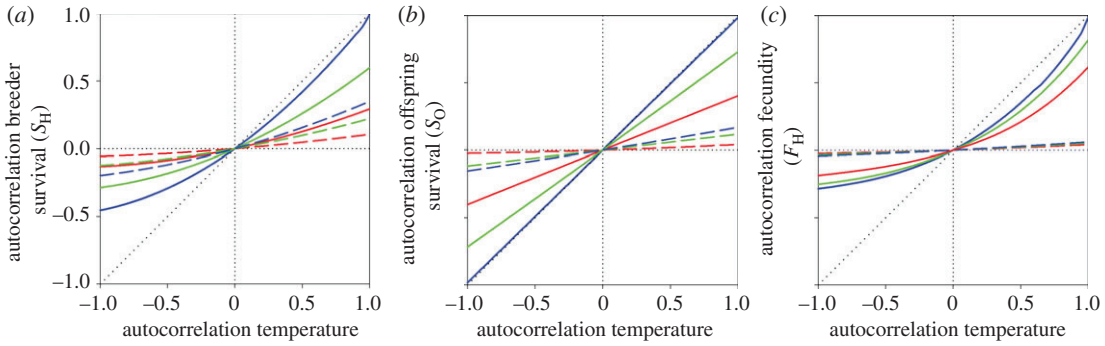

Figure 4. Environmental tracking by the demographic rates (*a*) breeder survival, (*b*) offspring survival and (*c*) fecundity, which each depend in alternative ways on temperature (respectively, concave, linear and convex dependencies; figure 1*b*). Solid lines refer to a situation where we assume that winter temperature explains 100% of the between-year variation in each demographic rate, while dashed lines refer to a situation where residual temporal variation in demographic rates is included (54–68% of the between-year variation in demographic rates was not explained by winter temperature [35]). Differently coloured lines show how the environmental tracking depends on population size: blue line, $n = 1000$; green line, $n = 20$; red line, $n = 5$.

finally decreased at large values of negative autocorrelation (figure 2*d*).

(c) *Relative effects of the colour, interannual variability and mean of temperature on extinction risk*

The autocorrelation, the interannual variability and the mean of winter temperature only varied over a specific range of values over the past 275 years (figure 2*a–c*), therefore, we primarily focused on the sensitivity of time to extinction over this range of conditions (grey areas in figure 2*d–f*). Although noise colour affected extinction risk, time to extinction was much more sensitive to changes in the interannual variability as well as to changes in the mean of winter temperature (compare slopes in grey areas between figure 2*d–f*). This pattern was consistent when looking at the time to extinction of 50, 10 or 1 per cent of all simulations (figure 2*d–f*).

The relatively weak effect of temperature noise colour on extinction risk was not restricted to the specific parameter conditions observed during our study period. The effect remained weak over a wide range of conditions of interannual variability (figure 3*a*) and of mean winter temperatures (figure 3*b*). Furthermore, the effect of noise colour on time to extinction also remained weak when we varied the carrying capacity of the population (i.e. changed the maximum number of territories and initial numbers of birds; figure 3*c*).

(d) *Environmental tracking*

In this section, we describe the environmental tracking by breeder survival (S_H), offspring survival (S_0) and fecundity (F_H), because these are the demographic rates to which time to extinction is most sensitive [35]. Furthermore, focusing on these three demographic rates is sufficient to demonstrate our point, and similar results were obtained for other demographic rates.

Demographic rates poorly tracked the temperatures' autocorrelation and we identified three mechanisms responsible. First, nonlinear demographic responses filter the colour of the environment: breeder survival and fecundity, both depending nonlinearly on winter temperature (figure 1*b*(i, iii)), had a whiter spectrum than winter temperature (solid blue lines in figure 4*a,c*). Blue

temperature noise is particularly strongly whitened over its entire range, while red temperature noise is only slightly whitened. By contrast, the linear demographic response of mean offspring survival to temperature (figure 1*c*) did not filter the noise colour (solid blue line in figure 4*b*).

Second, the presence of other sources of environmental variation (besides winter temperature) in mean demographic rates reduces the potential for environmental tracking. To illustrate this mechanism, we compared a situation where either all (solid blue lines in figure 4) or only part (dashed blue lines in figure 4) of the environmental variation in mean demographic rates was caused by temperature effects (by specifically excluding residual environmental noise, see §2). The presence of substantial residual environmental (white) noise strongly reduces environmental tracking, as fecundity was shown to be almost completely white over the entire range of temperature autocorrelations (figure 4*c*). Qualitatively similar results were obtained when residual environmental noise was assumed to be blue or red (not shown).

Third, the capability of demographic rates to track the colour of the environment declines with population size. Whitening of demographic rates by demographic noise primarily occurred at population sizes lower than approximately 50 individuals in our model, while the degree of whitening was very strong at population size below approximately 20 individuals (compare differently coloured lines in figure 4).

4. DISCUSSION

We showed that a key climatic variable has changed its colour during recent centuries from blue to red in The Netherlands. Our results for a Dutch oystercatcher population suggest that environmental noise reddening may increase extinction risk, but the relative impact of noise colour over the range of historically realistic values of autocorrelation is likely to be very small compared with the impact of other key aspects of environmental noise. Thus, our results do not support the hypothesis that extinction risk is more sensitive to environmental autocorrelation than to variability [37]. Extinction risk was relatively insensitive to noise colour, and we suggest that this is mainly owing to poor environmental tracking by demographic rates. In the remainder of the paper, we first discuss what determined how extinction risk changed with noise colour in our model. We then discuss the three mechanisms responsible for the poor environmental tracking and argue that they are likely to be important in many species. We argue that the common practice of assuming perfect environmental tracking may result in an overemphasis of the importance of noise colour for extinction risk. Finally, we discuss possible consequences for the practical application of population viability analysis.

(a) *How does environmental noise colour affect time to extinction?*

In a simple population model with linear dynamics, the extinction risk is expected to increase in red and decrease in blue environments [7,12], even if the stationary variance of the environment is kept constant. Our model has many complicating factors inspired by biological realism, specifically density dependence and a structured life history. Still, within the historical range of autocorrelation values, our results qualitatively follow the predictions from the simple model (figure 2). However, in extremely blue environments, extinction risk increases in our model, probably because the more frequent and strongly alternating sequences of good and bad years lead to catastrophic extinction in our model. The complex life history of oystercatchers is also likely to have played an influential role. For example, the different noise-filtering properties of various demographic rates suggest that blue environmental noise affects the environmental variance of population growth via different demographic rates from red noise (see §4*b*). Thus, the exact mechanisms underlying population dynamics in our model are complex, but understanding all details of the dynamics at extreme values of autocorrelation is beyond the aims of this study.

(b) *Environmental tracking and nonlinear demographic responses*

Laakso *et al.* [25] modelled how various types of nonlinear demographic responses to environmental variables may filter the noise colour. Their results are confirmed by our study, which shows that blue noise is particularly strongly whitened by the concave and convex responses of oystercatchers' breeder survival and fecundity, respectively (figure 4). Such filtering occurs because concave and convex functions level off at high or low values, which in both cases constrain the filtered signal from taking as extreme values as the input signal (*sensu* diminishing returns). Blue noise is thus expected primarily to affect oystercatchers' extinction risk through demographic rates with linear demographic responses, while red noise can also act strongly via demographic rates with nonlinear responses. However, more steeply convex or concave functions would also be expected to whiten red noise more strongly, while demographic rates that peak at intermediate values of the environment may even cause the colour of demographic rates to be opposite to that of the environment [25].

Nonlinear filtering thus has the potential to promote but also hinder population persistence. Yet, virtually all studies (see §1) that investigate the impact of environmental noise colour on extinction risk or on the population growth rate have ignored this issue, because they did not explicitly model how environmental noise affects demographic rates. To our knowledge, the only exception is the study by Griebeler & Gottschalk [24], who explicitly modelled how between- as well as within-year autocorrelation in temperature affected extinction risk via its effects on demographic rates. They did not report how well demographic rates tracked the colour of environmental noise, but interestingly their study also showed that extinction risk was not very sensitive to changes in between-year autocorrelation (relative to changes in within-year temperature correlation).

Nonlinear demographic responses are likely to be present in many species and thus we expect this mechanism of noise filtering to occur generally. A practical limitation is that long time-series are needed to be able to detect nonlinearities statistically. Potentially, general life-history properties of different species can be used to predict the shape of demographic responses [34] and thereby its filtering properties. In species with low reproductive

output, many individuals typically do not produce any young at all in normal years (average environments). Thus, in such species, fecundity cannot get much worse in bad years, whereas it can get much better in good years, resulting in a convex demographic response. It can similarly be argued that survival responses are typically concave for long-lived species (annual survival close to 100%), while for short-lived species (survival approx. 50%) the demographic response might be more linear [35]. Furthermore, the temperature dependency of many chemical processes might also contribute to the nonlinear dependency of demographic rates to climatic variables, especially in exotherms [50]. Life history and physiology might thus provide information about how sensitive species are to different aspects of environmental variables.

(c) *Environmental tracking and multiple environmental drivers*

In the wild, single environmental variables rarely explain more than 50 per cent of the between-year variance in mean demographic rates, and usually much less [26,35,51–53]. Demographic rates in most species are therefore likely to be influenced by a multitude of (a)biotic environmental drivers. When one specific environmental variable changes colour, other key environmental drivers (of any colour) are unlikely to change colour synchronously, and we have shown that this can buffer how noise colour affects the colour of demographic rates and thereby extinction risk. Other environmental drivers—even if not specifically identifiable—are thus important to consider in population models (as residual temporal noise in mean demographic rates). To our knowledge, our study is the first to address this issue, which in its most extreme case resulted in the colour of a demographic rate being almost insensitive to temperature noise colour (figure 4*c*).

Laboratory experiments on protozoa have shown that population fluctuations can track manipulated environmental colours to some extent [54,55]. However, this result may be unrepresentative for natural populations, because the laboratory conditions were probably designed to suppress other environmental drivers. Laboratory experiments have also highlighted that even in uncorrelated environments, the population numbers are typically autocorrelated owing to intrinsic properties of the population process (density dependence, stage-structure [56]). Thus, empirically measuring how the colour of demographic rates (or of population time-series) depends on the environmental colour introduces a whole new range of complexities.

(d) *Environmental tracking and demographic noise*

In large populations, environmental noise can cause populations to decline to levels where extinction risk strongly increases. At low population size, demographic noise owing to chance effects becomes increasingly important and can even outweigh the effects of environmental noise on population fluctuations [12]. This might hold particularly for oystercatchers, which seem to have a low environmental variance of population growth compared with other avian species [57]. More generally, the relative importance of environmental and demographic stochasticity on dynamics is expected to vary between species as a function of general life-history properties [57]. Demographic noise is not necessarily completely white, as individual heterogeneity can cause demographic rates to be correlated in time [58]. Nevertheless, any demographic noise is expected to reduce the ability of demographic rates to track the colour of the environment at low population size in all species (figure 4).

The importance of demographic noise potentially also depends on the exact biological mechanism generating demographic stochasticity, as different mechanisms may cause the demographic variance of population growth to increase less or more strongly with decreasing population size. Earlier studies have used various ways of modelling demographic noise (e.g. [11,16,17]). We included demographic stochasticity directly for each demographic rate by assuming that the realized individual reproduction and survival in a given year were generated by, respectively, a Poisson and binomial processes (as in [15,58]). We think this approach is realistic because the observed within-year variation in oystercatchers' demographic rates fitted these distributions well.

Since our simulated populations could fluctuate for long periods at low population size (see [35] for population trajectories), demographic noise is likely to have buffered the impact of environmental colour on the predicted time to extinction of oystercatchers. Demographic noise may have less influence on dynamics in species where one bad year can catastrophically reduce numbers from large population size to zero. In fact, many modelling studies on effects of environmental noise colour have specifically focused on population dynamical models that allow for catastrophic extinction [16], which may explain why the importance of demographic noise has not been specifically identified earlier. Nonetheless, the few available population time-series of recent local extinctions suggest that extinctions are typically not catastrophic, but instead result from gradual declines [12], suggesting that demographic stochasticity may buffer the effects of environmental noise colour in many species.

(e) *Ignoring environmental tracking*

As argued above, environmental tracking might be poor in many species, because each of the three mechanisms responsible is likely to be general. Consequently, previous studies potentially overemphasized the importance of noise colour on extinction risk and population dynamics, because they did not explicitly consider (i.e. model) how temporal autocorrelation in the environment translates into autocorrelation in demographic rates, and thereby implicitly assumed perfect environmental tracking (but see [24]).

(f) *Extinction risk: environmental autocorrelation versus variability*

Tuljapurkar & Haridas [37] made an important theoretical contribution by modelling the relative effects of environmental autocorrelation and variability on population dynamics. In their models, the population growth rate was often more sensitive to environmental autocorrelation than to interannual variability, and they hypothesized that the same may hold for extinction risk. By contrast, our

study—the first to our knowledge to specifically look at extinction risk—suggests that extinction risk is less sensitive to environmental autocorrelation than to interannual variability (figure 2). Our model differs in several ways from that of Tuljapurkar & Haridas [37]: specifically, we included demographic stochasticity, density dependence and environmental tracking as well as a different stage structure. Although the type of density dependence and stage structure may also influence how autocorrelation affects the population dynamics [56], the poor environmental tracking suggests that it is unlikely that these mechanisms alone caused the large differences in relative impact of variability and autocorrelation of the environment on extinction risk. Notwithstanding, direct comparison of outcomes between studies is difficult, and future studies on different species and models will have to show whether environmental tracking generally affects whether extinction risk is less sensitive to environmental autocorrelation than to variability.

(g) *Is white noise a poor null-model for population viability analysis?*

Many environments have a red spectrum [2,3], which implies that white environmental noise is typically not a good null-model [1]. Notwithstanding, most population viability analyses on threatened species still explicitly or implicitly assume a white environment [59], which has led to assertions that this might produce excessively optimistic assessments of population viability [1,15,21]. Although we agree that white noise is often a poor null-model for environmental noise, our results suggest that coloured environmental noise does not necessarily have large consequences for the temporal variation in demographic rates. Furthermore, accounting for the red colour of temperatures during the oystercatcher study period resulted in an only 3 per cent shorter predicted median time to extinction compared with assuming a white environment (399 versus 412 years; figure 2*d*). Consequently, if environmental tracking is equally poor in other species, the common practice of ignoring environmental autocorrelation in population viability analysis might be less problematic than generally thought.

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